

the brain was severed from the spinal cord some little way behind the medulla before I commenced its study. Into the circle of Willis the carotids enter rather far back; and in front of them, but still behind the sylvian artery, there was an ophthalmic artery, as I presume it to be, on the right side only: I found no trace of one on the left. A remarkable feature about the circle of Willis of this Hyæna is the great length of the anterior communicating artery, which lay in a loose circle posteriorly. Generally speaking, this artery is short and straight.

The *iliac arteries* in the specimen of *Galidia* were not symmetrical, as they are stated to be by Mivart* in other *Æluroidea*. The two larger external iliacs are produced by the terminal final bifurcation of the aorta. From the left of these arises a trunk which continues for a short distance in the same straight line as the aorta and then divides into the two internal iliacs. It is perhaps worth while mentioning that I found an asymmetry the precise converse of this in a Squirrel (*Sciurus prevosti*). In this animal the aorta ended in the same way, by dividing to form the two external iliacs. From the right of these arose a branch which shortly divided to form the two internal iliacs.

3. On the Postcaval Vein and its Branches in certain Mammals. By FRANK E. BEDDARD, M.A., F.R.S., F.Z.S., Prosector to the Society.

[Received April 8, 1909.]

(Text-figures 132-139.)

In studying the venous system of a large number of Mammals at the Prosectorium at the Zoological Society's Gardens I have relied entirely upon naturally injected veins. And indeed veins turgid with their own blood are better for this study than artificial injections. For, in the first place, error is absolutely eliminated, inasmuch as no injection-fluid can escape and give rise to apparent branches which have no existence; and, secondly, it is always possible to press upon the contained blood, and thus ascertain the reality of anastomoses, which can be readily missed in a defective artificial injection. Moreover, in animals which have died with their veins full of blood, minute branches which might be missed in other specimens, and which might not be reached by an artificial injection, are plainly revealed. I have, therefore, in the present communication only dealt with those out of the many specimens which I have dissected during many past years that were in a good condition for this particular study, and have rejected the data derived from anæmic examples. Thus I have every reason to believe that the facts which I now bring before the Society are accurate. It is now well known

* P. Z. S. 1882, p. 515.

that the venous system of Mammals, even as concerns the large trunks, is subject to considerable variation. It is, therefore, not without usefulness merely to record the facts alone as a contribution to this department of anatomical study. I have, however, referred to previous work upon the subject, and have endeavoured to summarise the present state of our knowledge upon the postcaval veins of Mammals and their branches. The important work of Hochstetter*, and more recently of McClure† and others, upon the venous systems of Edentates and Marsupials has attracted a great deal of attention to the venous system, and has been productive of definite ideas as to the arrangement of the several trunks in these animals. I am able to confirm, and in some respects to slightly extend, the work of these writers.

In making observations and in deducing conclusions from the arrangement of the veins in Mammals it is requisite to bear in mind the variability of these vessels, which appears to be greater than that of the chief arterial trunks. Recently the variability of the postcaval and its branches has been studied by McClure in the Virginian Opossum (*Didelphys marsupialis*)‡, by William Darrach in the common domestic cat§, and by H. von W. Schulte in various Marsupials||, while I myself have recorded¶ some variations among the Carnivora. I am able in the present communication to note some variations as well as normal arrangements. But inasmuch as variation occurs so frequently in so fixed a type as the Carnivore *Felis*, a specialised race of a specialised group, it is probable that variation occurs pretty well everywhere. But in the centre of this variation lies a mean which can be derived from the study of many examples.

§ *The Postcaval Trunk and its Branches in various Orders of Mammals.*

The **Marsupials** show a very constant condition in that the postcava lies medianly ventral to the aorta, so that on dissection the aorta is not seen, being completely covered by the postcava. The discovery of this very nearly universal characteristic of Marsupials we owe, as Hochstetter has pointed out**, to Owen††. After examining *Macropus giganteus*, *M. bennetti*, *Phascologomys wombat*, *Phalangista vulpina*, *Didelphys lanigera*, *D. pusilla*, *Phascologale penicillata*, *Belideus sciureus*, *Cuscus* sp., *Hypsiprymnus* sp., and two pouch-young of *Petaurus tugaroides*, Hochstetter found that this generalisation held good for all those species with

* "Beiträge zur Entwicklungsgeschichte des Venensystems der Amnioten," Morph. J.B. 1893; and "Monotremen und Marsupialier," in Semou's 'Forschungsreisen in Australien,' Bd. ii. Lief. 3, 1896.

† Amer. Journ. Anat. vol. ii. 1903, and vol. v. 1906.

‡ *Loc. cit.*

§ "Variations in the Postcava . . . in 605 Examples of the Domestic Cat," Amer. Journ. Anat. vol. vi. 1907, Anat. Rec. p. 30.

|| *Ibid.* p. 34.

¶ "On the Anatomy of *Galidia*," P. Z. S. 1909, p. 486.

** *Loc. cit.* p. 626.

†† 'The Anatomy of Vertebrates,' vol. iii. p. 552.

the exception of the last-named, *Petaurus taguanoides*. In that species he found that the postcava lay to the right "as in the Cat." My own observations quite bear out those of Hochstetter, to whose list I am able to add a few species dissected by myself which that anatomist had not the opportunity of examining. I have never met with the condition which characterises *Petaurus taguanoides* in any Marsupial.

In addition to these types, McClure, as has already been mentioned, has dissected many examples of *Didelphys marsupialis*, as well as the Wombat and *Petrogale* sp.*, while Parsons has reported upon *Petrogale xanthopus*†, and Parsons and Windle upon *Macropus rufus*‡. The figure of *Petrogale* given by McClure§ quite agrees with that of *Macropus bennetti* illustrating Hochstetter's remarks ||. In neither of these figures is the anterior spermatic veins represented, though McClure states that they are present, as also in the Wombat. They are furthermore represented by the last-mentioned anatomist in *Didelphys*¶, and the anastomosis between the anterior and posterior spermatic veins clearly shown. Inasmuch as McClure has remarked that in the Wombat the spermatic veins also open in the neighbourhood of the kidneys, as well as into the postcaval trunk, I do not quite understand his saying, in a later paper, that "In a number of adult Australian Marsupials, however, the spermatics do not open into the postcava, as in *Didelphys*, but open into it at the base of the renal veins, as in *Phascolomys wombat*, or into the renal veins themselves, as in *Notoryctes typhlops*," as observed by Miss Sweet**. It would appear, however, that McClure does not allow the value of a spermatic vein to a vessel often slender which does pass between the gonads and the renal vein; for he writes thus of *Didelphys*: "In none of the adults examined did the spermatics open into the renals, although an anastomosis between the latter and the spermatics was *invariably* †† present, on each side, in the form of a small vein which followed the ureter." As a matter of fact, I have myself generally found two such small veins which were frequently large veins fully as important as what I term the posterior spermatic veins, which open behind them into the postcaval itself. Nor, indeed, is any difference of size shown by McClure in the plate‡‡ which illustrates the main venous trunks (as well as the arterial) of *Didelphys virginiana*.

In a female *Trichosurus vulpecula* I found that the postcaval and its various branches were arranged as follows:—The asymmetrical renal veins not only lacked symmetry in their plan of opening into the postcaval trunk, but also in their number, for

* Amer. Journ. Anat. vol. ii. 1903, p. 388.

† P. Z. S. 1896, p. 683.

‡ J. Anat. Phys. vol. xxxii. 1898, p. 119. This paper deals mostly with osteology, muscles, and viscera. But the authors mention the ventral position of postcaval.

§ *Loc. cit.* p. 388, fig. vi.

|| *Loc. cit.* p. 626, fig. 13.

¶ Amer. Journ. Anat. vol. v. 1906, p. 199.

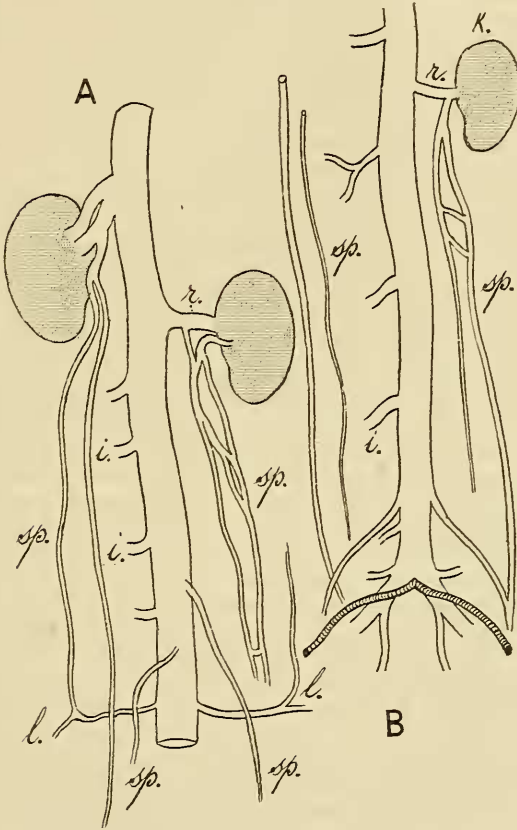
** Proc. Roy. Soc. Victoria, vol. xvii. 1904, pt. i.

†† Italics Dr. McClure's.

‡‡ Amer. Journ. Anat. vol. v. 1906, pl. i.

on the right there were two of these veins of equal and considerable size. On the left only a single renal vein debouched into the postcava. As is usual (? universal) among Marsupials both renal veins give off an ovarian vein, in addition to that pair which flow directly into the postcaval. On the right side a single

Text-fig. 132.



Postcaval vein and its branches in *Trichosurus vulpecula* (A) and *Trichosurus fuliginosus* (B).

i. Intercostal veins. *K.* Kidney. *l.* Lumbar veins. *r.* Renal veins.
sp. Spermatic or ovarian veins.

vein opened into the lower of the two renal veins; at a little distance from its point of opening into the renal vein this ovarian vein divided into two. Of these the outer branch opened into the lumbar parietal some little distance away from the opening

of the latter into the postcaval. The inner vessel, running of course parallel with the outer branch, crossed over the lumbar and reached the ovary. There was no junction between this vein and the main ovarian trunk, which I shall describe directly as opening straight into the postcaval, except perhaps quite distally, where the smaller branches of both these veins may anastomose on and about the ovary.

On the left side the veins in question were somewhat different. There are, however, two of them, as on the right side. Anteriorly these two veins cross and anastomose with each other more than once, and one of them appears to be connected directly with the kidney of the left side. Posteriorly the two vessels are again united by a short transverse trunk on a level with the posterior ovarian veins. Both these vessels appear to reach the ovary. With the left lumbar parietal vein is connected a forwardly running branch, as on the right side. It occupies an entirely corresponding position, but does not form either of the ovarian veins just described. It gradually dies away anteriorly. Between the left renal vein and the lumbar already spoken of are four intercostal veins. On a level with the last of these and rather asymmetrically (the left being in front of the right) enter the posterior ovarian veins.

Of a few other Marsupials I have less complete notes upon these various veins. In a specimen of *Trichosurus fuliginosus** the two renals were very asymmetrical, the left being much below the right in its point of entry into the postcaval; the two anterior spermatic veins were present, and the left certainly, and the right probably, flowed into each renal. Whether they anastomosed with the posterior spermatics I am not certain, but I think that they did not. The latter veins were also asymmetrical, the right opening into the postcaval below the left.

A second example of *Trichosurus fuliginosus* showed some additional features of which I had not made notes in the first example. The asymmetry of the posterior ovarian veins seems to me to be explained by this specimen. When the right vein is carefully examined it is seen not to enter the postcaval, where it appears to enter, *i. e.* just opposite to the entry of the left ovarian vein. From this point it runs forwards, closely adhering to the postcaval vein until it reaches the next intercostal vein, in common with which it opens into the postcaval. Whether there is or is not a connection also with the intercostal lying next behind the one just referred to—and I am inclined to think that there is—we have here, as I believe, a retention of a more anterior section of the postcardinal than is retained on the left side. This appears to be shown by the course of the vein strictly parallel to and in close contact with the postcaval (*i. e.* the right subcardinal,

* In all the species which I describe here the postcaval lies below (*i. e.* accurately above, on a dissection from the ventral surface) the aorta. This fact, clearly unusual among Marsupials, was first discovered by Owen, as both Hochstetter and McClure have pointed out in their memoirs.

or both cardinal collaterals*) and its connection with a vein of the body-wall.

On the left side two vessels run, one on each side of the ureter to the renal vein of that side into which they opened after fusing into one vein. Lower down, these vessels were connected by several cross-anastomoses. The outer of the two, which is the real anterior ovarian vein, anastomoses with the posterior ovarian vein only just in front of the ovary. The inner and more slender of the two vessels could be distinctly seen to pass dorsally of the posterior ovarian, and to follow the ureter to the bladder. On the right side the outer (ovarian) vessel did not fuse with the posterior ovarian, but passed dorsally to it. I did not follow the more slender vessel beyond the posterior ovarian. Between the left renal vein and the posterior bifurcation of the postcaval were four stout intercostal veins, of which two lay above the entry of the right ovarian, which enters the postcaval in common with the third of these four veins. The lumbar parietal veins flow into the common iliac vein on either side. The ovarian arteries escape from the aorta just at the bifurcation of the postcaval, as shown in text-figure 132, p. 499.

In *Pseudochirus peregrinus* the veins in question are much like those of *Trichosurus vulpecula*, but show differences of detail. The renals are but slightly asymmetrical. Into each renal opens a vein at right angles, which is compounded of two running along the ureters. These become separate at a very short distance from the renal vein. They appear to cross the spermatic vein without forming an anastomosis with it, and they do not anastomose with each other. The spermatic veins are symmetrically paired and flow into a postcava some way below the renals. There are two intercostal veins lying between the influx of the spermatics and the left (lower) renal. On one side of the body I noted an anterior lumbar parietal vein, which passes along the lower border of the kidney at right angles to the anterior spermatic vein, from which it arises close to the renal vein. The posterior lumbar parietal veins flow perhaps rather into the iliacs than directly into the postcaval stem, but are just at the junction of the two.

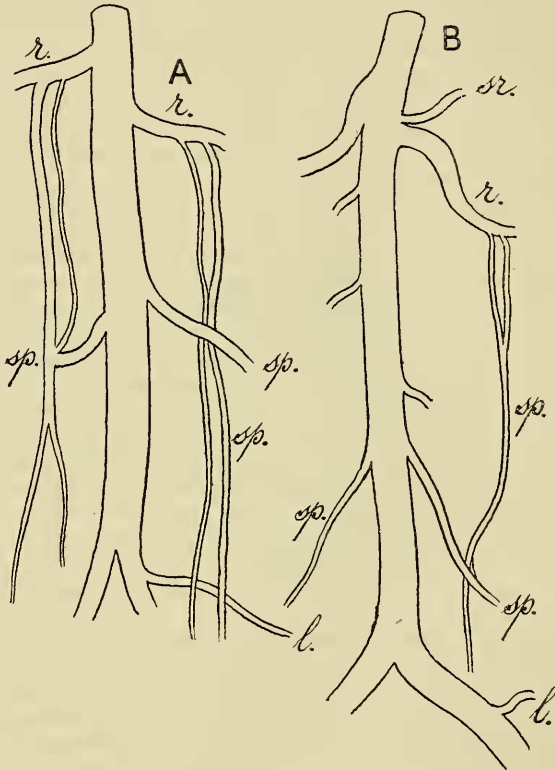
In *Onychogale lunata* both anterior and posterior spermatics were present, though I am uncertain as to an anastomosis between them. The posterior spermatics were very asymmetrical, the left being much above the right. The latter, indeed, joined the postcaval only just in front of the bifurcation to form the iliac veins. The renals were also as usual asymmetrical.

In *Onychogale frenata* the typical Marsupial arrangement was met with in all its essentials. There were nevertheless slight differences in detail between these two Marsupials. The renal veins although asymmetrical were not very much so, the right-

* It is impossible to fix accurately, without embryological data, which part of the postrenal section of the postcaval is here dealt with.

hand vein being only slightly above the left. The individual dissected was a rather large young one, but from the pouch; but it does not appear likely that it would have retained any foetal characteristics. On each side the usual two veins open into the renal. One of these, the outer renal, seems to open directly into the kidney, as I have noticed in *Trichosurus vulpecula*. The two veins do not form any anastomoses that I could detect, and neither of them become connected with the posterior spermatic veins. The latter are quite symmetrical. The left suprarenal vein opens into the renal vein just before the latter debouches into the postcaval.

Text-fig. 133.



Postcaval vein and its branches in *Dasyurus maugai* (A) and *Onychogale frenata* (B).

sr. Suprarenal vein. Other lettering as in text-fig. 132.

In another specimen of *Onychogale frenata* there were some slight differences. This example was an adult female with a small young one in the pouch. The renals were perhaps rather

more asymmetrical. Both renals, it ought to be stated, were single veins, as in the last specimen. The suprarenal of the left side entered the postcaval just at its junction with the left renal. The posterior ovarian veins were nearly but not absolutely symmetrical, the right-hand vein being just a shade above the left. The anterior ovarian veins were double on each side, and certainly anastomosed with the posterior ovarian on each side, where they passed dorsal to it. The two veins—closely following the ureters, as is the case in other Marsupials—were connected to each other by numerous anastomoses, and the conditions were the same on both sides of the body. Between the entrance of the renal vein (left) and the point of entrance of the two posterior ovarian veins I counted three rather slender intercostal veins, of which two were distinctly on the right side of the postcaval, and one (the last) as distinctly on the left side. The lumbar parietal veins opened into the iliac a considerable distance from the bifurcation of the postcaval, and were directed anteriorly in their course.

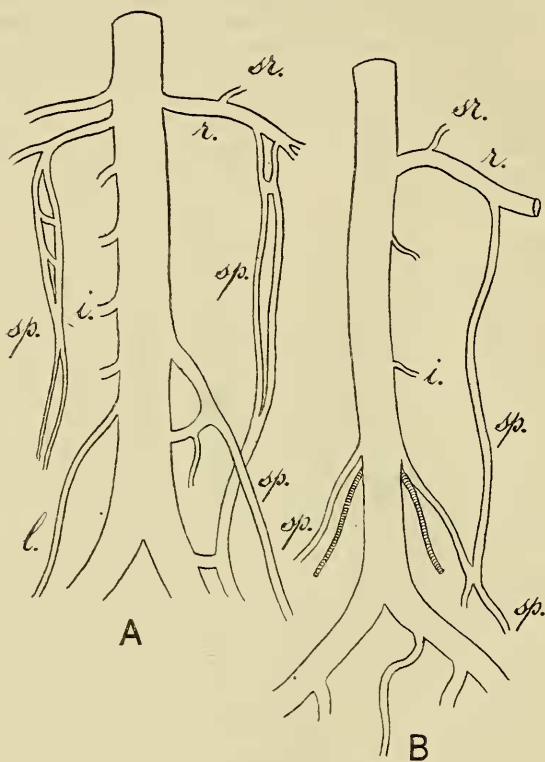
In *Macropus parryi* the typical Marsupial conditions are met with. The example which I dissected was in very good condition for the examination of the veins; for these vessels were turgid with blood and the smaller branches could be followed with ease. The renal veins are roughly symmetrical: there were two of them on the right side and one on the left; the left renal vein divided into three before entering the kidney. The ovarian and its parallel vessel, which empty themselves into the renal vein on either side, were well developed, and each couple of vessels were connected by more than one anastomosis. I am not quite certain whether they were also connected with the posterior ovarian veins flowing into the posterior part of the postcaval. In any case the connection must be by means of minor twigs; for the main vessels could be seen easily to pass dorsally to the posterior ovarian trunk on each side on their way from the generative organs. One of the two anterior ovarian veins becomes connected by a transverse branch with the common iliac vein just before the union of the latter with its fellow to form the postcaval.

The position of this vein, which runs transversely into the iliac, is very suggestive of the posterior lumbar parietal vein of other Mammals. It is, however, certain that in the present species the vein does not bring back blood from the parietes; it is merely a junction as already described. I could not find a vein corresponding to this on the right side. The left suprarenal vein had an antero-posterior course opening into the left renal. The two posterior ovarian veins were asymmetrical, the left joining the postcaval considerably higher up than the right. The left vein had furthermore two branches, also connecting it with the postcava lower down. The lowermost of these was a stout branch which gave off a backwardly running twig to the parietes; it may be that this vessel is really the homologue of the lumbar parietal above referred to. I noticed nothing of the kind in

connection with the right posterior ovarian vein. Between the right renal and the right posterior ovarian vein four median intercostal veins opened into the postcava. These veins appeared to me to be particularly slender.

In *Macropus hagenbecki* the renals were nearly symmetrical, and so also were the posterior spermatics; the anterior spermatic veins were present.

Text-fig. 134.



Postcaval vein and its branches in *Macropus parryi* (A) and *Macropus agilis* (B).

In the latter the spermatic arteries are shown emerging from the concealed aorta just below the posterior spermatic veins.

Lettering as in text-figs. 132, 133.

Macropus agilis agrees very closely with *M. parryi*. The left suprarenal flows into the left renal near to its entrance into the postcaval. The two vessels accompanying the ureter appeared to me to anastomose, one of them at any rate and that on the left side, with the posterior ovarian vein. The posterior ovarian veins

were symmetrical and had no secondary connections with the postcaval*. The intercostals were very slender as in *Macropus parryi* and apparently paired at their entrance into the postcaval. Into the left common iliac opened a medianly situate caudal vein. The ovarian arteries, contrary to what I have recorded in *Trichosurus fuliginosus*, emerged along with the ovarian veins. On the left side I counted two intercostal veins between the renal and the posterior ovarian.

Dasyurus maugei (see text-fig. 133 A, p. 502) shows some slight variations in the postcaval branches, which do not, however, in any way detract from the quite typically Marsupial arrangement of the veins in that animal. I have examined most of these veins in five examples. The renal veins in all were symmetrical, the right being considerably in advance of the left. The posterior spermatic veins were also very nearly if not absolutely symmetrical. The usual two veins on each side entered the renals; but in one specimen at any rate the outermost of these veins seemed to enter the kidney itself, there being thus a kind of suggestion of a renal portal system. I have noticed this same connection with vessels actually within the kidney in other animals, and it may possibly be the persistence of an embryonic condition. The importance of these anterior spermatic veins appears to vary in individuals, and I think that they do not always anastomose with the posterior spermatics. The left suprarenal sometimes opens into the left renal and sometimes into the postcaval vein direct.

Among the **Edentata** I have chiefly examined the Dasypodidæ. It is already clear from the investigations of Hochstetter that the genus *Dasypus* is characterised by a postrenally divided postcava. Two species figured and described by Hochstetter † (whose figures are copied by McClure ‡), viz. *D. setosus* and *D. novemcinctus*, differ, however, in certain details. In *Dasypus setosus* the postcava is double at an earlier position than in the other species of *Dasypus*. Immediately after the embouchure of the two renal veins the postcava is divided in *D. setosus*. The division occurs lower down in *D. novemcinctus*. Moreover, in the former species another character of this genus is shown in a more marked fashion, i. e. the caudal vein forms a more complex rete of vessels. Finally, while in *D. setosus* only the left renal vein is double, both are double in *D. novemcinctus*. These peculiarities may of course be individual. In the generalities of the disposition of the veins concerned I can assert that *Dasypus vellerosus* resembles its congeners. There are, however, differences of detail which are worth noting, though some of them may of course be individual.

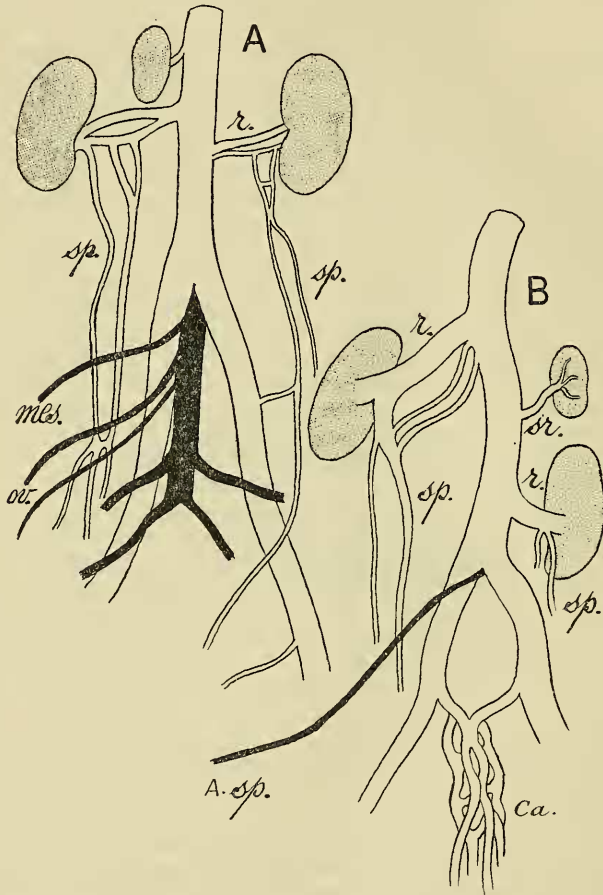
* It seems probable that the secondary connections described above in *Macropus parryi* are explicable on the same grounds as those urged in explaining the asymmetry in *Trichosurus fuliginosus*. The "connections" are probably to be looked upon as intercostal veins, and one of them (see text-fig. 134 A) has a branch to the parietes.

† Morph. Jahrb. t. c.

‡ Anat. Anz. xxix. 1906, p. 376, fig. 3, p. 377, fig. 4.

In *Dasypus vellerosus* (text-fig. 135 B) the renal veins are asymmetrical. The right arise in front of the left, as is so very usual among the Mammalia. On the right side there is one principal renal vein. This is reinforced by two others, but

Text-fig. 135.



Postcaval vein and its branches in *Tatusia peba* (A) and *Dasypus vellerosus* (B).

A.sp. Spermatic artery. *Ca.* Caudal plexus. *mes.* Mesenteric artery.
ov. Ovarian arteries.

Other lettering as in text-figs. 132, 133.

these latter rather slender trunks do not reach the kidney by a direct route. They open into the larger of the two veins which arise in common from the principal renal vein and descend

along the ureter. Their course is thus somewhat oblique. In this we have an exact resemblance to *D. novemcinctus*. On the left side the renal vein is quite single (it is double in both of the species already mentioned) and it gives off just before entering the kidney two veins like those of the opposite side of the body. The left suprarenal vein enters the postcaval, just anteriorly to the influx of the left renal. The point at which the postcaval bifurcates is behind the renal veins and seems to me to be pretty well intermediate in position as compared with the two forms studied by Hochstetter. The rete formed by the caudal vein is large, as in *Dasyppus setosus*. It is a complex rete mixed up with the caudal artery in a way which I have not disentangled.

I have also had the opportunity of examining a fourth species of *Dasyppus*, viz. *D. villosus*. Of this species I have dissected two examples, but am only able to say something concerning the details of the postcaval vein in one. Of the other I can only say that it showed the typical condition of this genus. It is of course important even to say this. For in some mammals which show a double postrenal postcaval (e. g. *Ictonyx* *) there is variation, some examples being normally Eutherian without a postrenal doubling. In one example of *D. villosus* the veins in question were simpler than in the other types hitherto dealt with. The renals were asymmetrical as in the others; but there was only a single renal vein on each side. These two veins appeared to me to be of about the same size. The left suprarenal vein entered the left renal only just before its connection with the postcaval. From each renal arose a single ovarian vein descending parallel to the longitudinal axis of the body as in the other species. On both sides the lumbar veins were two, opening each into the divided region of the postcaval. I did not note these veins in the other species.

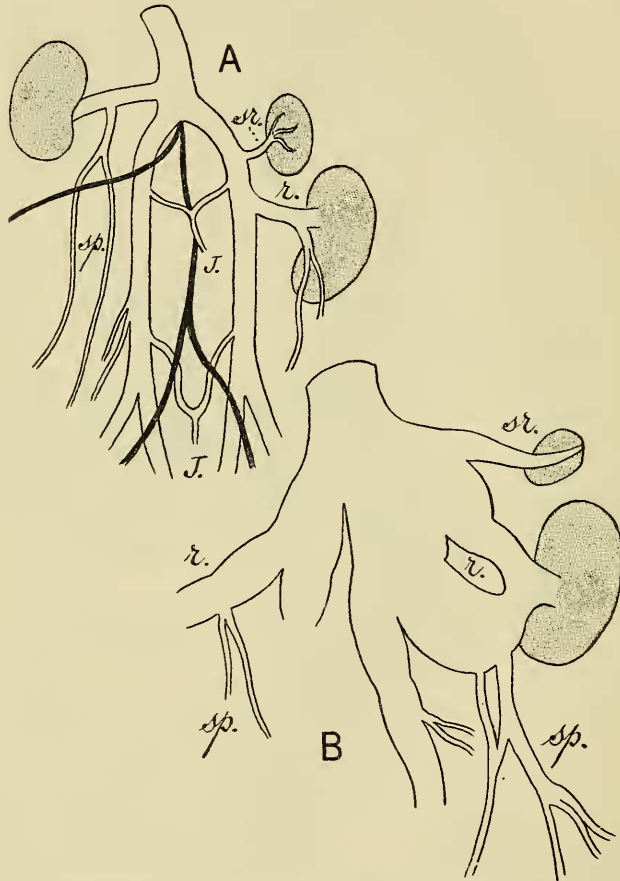
I am also able to add to what is known concerning the postcaval vein and its branches in the Armadillos some notes upon these veins in *Lysiuirus unicinctus*, a species of which I have dissected one example which was a male. In this Armadillo the division of the postcaval is more marked than in any species of *Dasyppus* (among those referred to in the present communication). The division just extends anteriorly to the influx of the renal veins; and the conditions which obtain in this genus are therefore like those which occur in *Mephitis* † occasionally, where, however, it is only one renal (the left) that opens into the divided portion of the postcaval. In the Armadillo with which I am now concerned both renal veins are thus separate from each other. Another noteworthy point about this species is the greater calibre of the renal vessels on the left side of the body as compared with those of the right. They were vast in the specimen which I dissected and turgid with blood. On the left side of the body

* Cf. Beddard on *Galidia* &c., P. Z. S. 1909, p. 491.

† P. Z. S. 1909, p. 492.

there are in fact two renals, of which the lower is the larger; the two join before entering the substance of the kidney and may be also said to rejoin before entering the left half of the postcaval vein. The diameter of the lower renal is greater than that of the postcaval into which it flows. The left suprarenal vessel just

Text-fig. 136.



Postcaval vein and its branches in *Centetes ecaudatus* (A) and *Lysiusurus uncinatus* (B).

J. Junction between two postcavae in *Centetes*.

joins the upper renal vein before the latter joins its fellows. From the lower renal vein two veins arise, of which the outer is the spermatic; it soon divides into two trunks, but just before this

sends off a branch to the inner vessel which runs along the ureter. On the right side the renal vein was quite single. With it are connected two veins as on the opposite side; but these as well as the renal vein were of less calibre than their fellows on the left. I noticed a double lumbar parietal vein on the left side; but have no notes concerning a corresponding vein on the right. I also observed a caudal plexus in the pelvic region, which is so characteristic a feature of the venous system of the genus *Dasyppus*. In the large tract of postcaval, which is double, it is clear that this species comes nearer to *Dasyppus setosus* than to the other species of that genus which have been described.

I did not find posterior spermatic veins in this Armadillo, and am sure that I have not confused such veins with the lumbar parietal veins already referred to.

I have already mentioned in a preliminary note* that the venous system of the genus *Tatusia* is constructed upon the same plan as that of the genus *Dasyppus*, instancing the species *Tatusia kappleri*. Of that species I have accurate notes upon the left side of the body only. The postcava is double at some little distance behind the influx of the renal veins and just in front of the origin of the ovarian arteries. The left renal vein is single and enters the postcaval behind and not in common with the supra-renal of its side. Just before the renal vein reaches the kidney, or, to speak more accurately, just after it has left the kidney, it gives off a descending branch which fuses with the ovarian vein to be described shortly and then bifurcates, one branch going to the ovary and the other passing down the ureter. The latter is connected with an ascending branch which I did not trace so far forwards as the renal vein, but it evidently corresponds to the second of two veins which debouch into the renal vein in other Armadillos. The ovarian veins are quite symmetrical, and, as in *Dasyppus novemcinctus*, as figured by Hochstetter, flow into each half of the postcava just after the bifurcation and on a level with the emergence of the posterior mesenteric artery.

Of *Tatusia peba* I have more elaborate notes. The individual which I dissected shows some differences from the specimen of *Tatusia kappleri* just described. The renal veins (see text-fig. 135 A, p. 506) are asymmetrical, but the left does not become connected with the postcaval a very long way below the right. The renal veins are not, however, single on each side as in *Tatusia kappleri* (? as to right side); there are two veins on each side, of which the more anterior is in both cases the larger. From the lower of the two renal veins of each side depend two veins which are again fairly symmetrical on both sides of the body. These are shown in the figure (text-fig. 135 A), and they will be seen to join and rejoin in a plexus-like fashion. The outer branch is ovarian and the two inner follow the ureter. I do not think that there are ovarian veins connected with these and with

* Amer. Journ. Anat. 1907, p. 111.

the main postcaval trunk. On one side I found a small vein which I regard as lumbar; but I could see nothing on the other side. On the other hand, an additional vein to the ovary was connected with the postcavals far down and in the pelvic region close to the ovaries. The postcaval becomes a double vein some way after the renals and the position of the point of bifurcation seems to be much as in *Tatusia kappleri*. I have no notes as to a caudal plexus in this Armadillo, and I do not think that I should have failed to note it were the plexus present. At the same time I feel unable to assert positively that it is absent.

It is clear, therefore, from what has been said and from a comparison of the facts which I am able to bring forward here with those noted by other observers, that the Armadillos as a family are to be characterised by the invariable presence of a divided postcaval, but the actual point at which the division occurs differs. Again, in all Armadillos the sexual veins are symmetrical and connected with the renals, while accessory veins to the gonads are not invariably present; when present they occur some way down the postcava and are symmetrical. The caudal plexus is not universal, but is characteristic of the genus *Dasyppus* alone of those examined.

While it appears to be clear, from the investigations of Hyrtl*, Hochstetter †, and myself ‡, that the divided postcaval vein is a distinctive feature of the Armadillos, occurring, without exceptions as to species or individuals, in all of the four genera which are at the present time known, the facts are otherwise among the **Insectivora**. In both *Erinaceus algirus* and *E. europæus* there is a single postcaval vein which is undivided until it divides in the usual way to form the two iliac arteries, or there may be (*E. europæus*) a divided postcaval as in *Centetes*. On the other hand, in the genus *Centetes* the postcaval vein is broadly as in the Armadillos, though, as will be seen presently, there are differences. In *Erinaceus algirus*—to commence with the simpler form seen in Insectivora—the renals are asymmetrical, the left lying, as is the rule in such cases, below the right vein. The left suprarenal vein opens into the left renal and just above the entry into the latter vein of the ovarian vein which runs down along the ureter. The corresponding ovarian vein of the right side enters the postcaval at a point about on a level with the entrance of the left renal: there is thus a kind of symmetry in the ovarian veins such as occurs in other animals, for instance in *Lagostomus trichodactylus*§, *Paradoxurus hermaphroditus*||, &c. The two lumbar parietal veins, so constant among mammals, open symmetrically into the iliac veins just below the partition of the postcaval.

In an example of *Erinaceus europæus* I observed a slight difference from the state of affairs here recorded in *E. algirus*, which I do not for a moment attribute to specific differences, but

* Denkschr. Ak. Wien, 1855.

† Morph. Jahrb. xx.

‡ *Suprà*.

§ *Vide* p. 516 of the present communication.

|| Beddard on *Galidia* &c., P. Z. S. 1909, p. 489.

rather regard as a mere variation of an individual character. In the European Hedgehog I found that the renal veins were quite or very nearly symmetrical. It ought also to be stated that the postcaval vein lay posteriorly to the right of the aorta, as is the normal position in Eutherian Mammals. In a second specimen there was a divided postcaval as in *Centetes*; but I am unable to give details.

In *Centetes ecaudatus* (see text-fig. 136 A, p. 508) I found the conditions characteristic of the Armadillos somewhat exaggerated. In a specimen of that Insectivore which I dissected some two years ago the postcaval was formed of two parallel vessels from a point slightly in front of the influx of both renal veins anteriorly. A larger region was therefore double that in *Dasyppus* &c. The renal veins were single on both sides, the complication of these veins so often seen among the Armadillos being in *Centetes* quite undeveloped. The two divisions of the postcaval after the influx of the renal veins were separated somewhat widely as in *Dasyppus* &c.; but this separation was not complete. For two veins bridged over the intervening space, as is shown in the figure (text-fig. 136 A). The first of these was slightly behind the left renal, and each slender vein joined its fellow to form a short backwardly running median vein. Further back still, just in front of the iliac veins, there was another small median vein formed by the union of two similar branches. The posterior mesenteric artery emerges from the aorta in front of the anterior bridge. The conditions thus shown are not seen in the Armadillos. But they exactly correspond (in that there are two bridges between the right and left postcavæ) to a stage in the development of these veins in *Echidna* figured by Hochstetter*, whose figures have been copied by McClure †.

Such anastomoses also occur in *Didelphys* as stated by McClure. It is perhaps, therefore, possible to say that the presence of such anastomoses uniting the postrenal section of the postcaval, which is, as I presume, formed at least more anteriorly by the two sub-cardinals of the embryo, is an archaic character; for during the development of *Didelphys* such anastomoses occur of which there are in that Marsupial, as already stated, frequent traces in the adult in various positions and of differing degree, many of which have been described and figured by McClure in his paper to which reference has been made so often in the present communication. But without actual developmental facts relating to *Centetes* it is of course dangerous to press any such comparisons very far. For it is equally possible that the anastomoses in question are a remnant of the cardinal collateral system. In *Centetes*, as in *Erinaceus* and other primitive mammals, each renal vein received from the hinder region of the body two veins which course along the ureter; one of these, as in other animals is the ovarian vein.

* "Monotremen u. Marsupialier," in Semon's Zool. Forschungsreise in Australien, Bd. ii. Lief. iii.

† Amer. Journ. Anat. ii. 1903, p. 400, fig. x.

The lumbar parietal vein of one side at any rate emerged from the parietes in a plexus form and entered the right half of the postcaval some distance below the entrance of the renal of the opposite side of the body and *a fortiori* below the entrance of the renal of its own side of the body. The left suprarenal vein is formed of three principal twigs which leave the suprarenal body; it enters the postcaval in front of the entrance of the left renal and not in common with that vein. It is therefore to be noted that in this animal the suprarenal and ovarian veins do not lie in the same straight line and present the appearance of being portions of the same original vein (the left posterior cardinal) as they do in various Marsupials. Although I am of my own knowledge unable to do more than state that one of the two examples of *Erinaceus europæus* which I dissected showed the divided postcaval characteristic of the Edentates, Monotremes, &c., the conditions which actually obtain in such a specimen with a divided postcaval have been figured and described by Hochstetter*.

This figure shows that the arrangement of the veins in *Erinaceus* is in some respects different from that which I have described and here figure in *Centetes* (see text-fig. 136 A, p. 508). They both agree, however, in that the division of the postcaval extends further forward than in the Armadillos. The postcaval is formed of two veins in both species up to a point just anterior to the opening into it of the right (and anterior) of the two renals. There appears, moreover, to be a junction between the two halves of the postcaval in *Erinaceus* corresponding to the posterior of the two transverse trunks of *Centetes*. Otherwise one is struck rather by the differences than by the points of likeness which the postcaval venous systems in these two types show to each other. The kidneys and their veins are more symmetrical in *Erinaceus*. From the left renal arises only a single vein, which is the ovarian of *Centetes*. It is unaccompanied in *Erinaceus* by a second vein coursing along the ureter. Moreover, this vein in *Erinaceus* anastomoses with a posterior ovarian vein as in the genus *Dasyurus* (in some specimens). The condition is, in fact, more "Marsupial" than is that of *Centetes*. On the right side there is no symmetry in the ovarian vein. It flows into the postcaval vein of its side, and not into the renal as in *Centetes*. It, however, joins the other ovarian vein below. It is to be noted that this example of *Erinaceus*, which Hochstetter speaks of as "abnormal" in the disposition of the postcaval vein, agrees in this last particular with a specimen of *Erinaceus algirus* examined by myself and reported upon in the present communication. For in the latter example the ovarian veins show precisely the same asymmetry. It is clear from the additional facts which I am able to bring forward in this paper, that the postcaval venous system of the Insectivora has not so completely rid itself of its primitive paired character as it has in the Carnivora, where apparently only vestiges

* Morph. Jahrb. Bd. xx. 1893, Taf. xxiii. fig. 24.

remain of the double postcaval*. The Edentata, Insectivora, and Carnivora can be arranged in a series in the order in which they have just been named in respect of the double character of the postcaval veins, *i. e.* the more or less complete persistence of both of the subcardinal veins or cardinal collateral veins. It is doubtless important to note that the Rodentia, which are equally primitive in the azygos veins, show no traces of any likeness to the Insectivora in respect of the postcaval.

The condition characterising the adult *Centetes* and Dasypodidae is also very well seen as a temporary feature of the foetal Mole. At a certain stage figured by Messrs. Soulié and Bonne †, there are two thick veins which unite inferiorly and which I presume represent the cardinal collaterals as described by McClure. A small branch of the renals which is not lettered by these authors seems to correspond to the real cardinals. Between the preserved cardinal collaterals (in the 12.5 mm. long embryo described by Soulié and Bonne), which are thick veins, is a medianly situated single vein of some calibre, which may perhaps be the equivalent of the subcardinals as described by McClure in the American Opossum, or possibly be the equivalent of the median prolongations of the commissural vessels in *Centetes*. This soon disappears as an important vessel, but remains as a slight commissure. The authors speak of the persistent postcaval as being formed in the postrenal region by the "right internal vein of mesonephros," which is not homologised with any particular division of cardinals. There seems also at a certain stage to be a caudal plexus which heightens the likeness to the adult Armadillo. The developmental phenomena argue at least a general similarity with other Mammals as described by other authors.

As to the *Ungulata*, I have examined the postcaval and its branches in several examples of *Hyrax capensis* and in one of *H. dorsalis*. The general arrangement in both species appears to be as follows:—The renals are asymmetrical as usual, the right opening into the postcaval above the left. The postcaval postrenally lies as usual to the right of the aorta. The ovarian vein on the left side opens into the renal, but on the right into the postcaval in line with the orifice of the left renal. There is thus a kind of symmetry between the two ovarian veins such as is met with in the Rodents, some Carnivores, &c. In one specimen (of *capensis*) I noted more particularly the branches of the right ovarian vein. This vein shortly after leaving the postcaval (it is simpler for purposes of description to disregard the direction of the blood-flow and to treat these affluents as branches) divided into two equisized veins. The anterior of these was directed forwards and ran along the body-wall giving off branches to the parietes. It ran about parallel to the postcaval and its course suggests an anterior section of the postcardinal. The

* See Beddard, P. Z. S. 1909, p. 491, text-fig. 131.

† "Recherches sur le développement du système veineux chez la taupe," Journ. de l'Anat. et Phys. xli. 1905, p. 1.

posterior branch ran in the same straight line as the anterior branch and divided into two principal trunks, of which the anterior supplies the ovary itself and the hinder the oviduct. In two other examples I found this branch just as plain. It is remarkable that it was at least not so obvious on the left side; indeed I made no notes at all as to its occurrence on that side of the body. It is possible that the restriction to, or at least the more marked development upon, the right side of the body is connected with the persistence of the right azygos vein only (as a rule) in this Subungulate.

McClure has discovered * the interesting fact that in *Tragulus meminna* the postcaval is divided postrenally as in Armadillos &c., and I have been able to confirm † him by the examination of three individuals. Since the publication of my note referred to I have examined two other examples of *Tragulus meminna* which presented an identical disposition of the vena cava posterior. Furthermore, I have still more recently dissected an example of *Tragulus stanleyanus* in which the same bifurcation of the postcaval occurred, and in the same way the genital veins arose symmetrically from the region of the postcaval.

The **Lemuroidea**.—In the course of some notes upon the anatomy of *Chiromys madagascariensis* ‡ I have pointed out that within the group of Lemurs considerable variations exist in the tributaries of the postcaval vein. It seems to me to be evident—though I did not point it out in the memoir to which I have referred—that *Microcebus* has retained the Marsupial and Edentate character in its venous system, in that the spermatic veins arose more or less symmetrically some way down the postcaval and that both were connected with the renal veins by a slender vessel on each side, which seems to me to represent the anterior spermatic vein of Marsupials, but in this Lemur (*Microcebus*) in the course of disappearance. On the other hand, in *Chiromys* (of which Lemur I reported upon two examples in the paper referred to and have here to report upon a third §) only the posterior spermatic veins in the male at any rate are left.

A study of the postcaval and its branches in *Lemur catta* shows that this region of the venous system is like that of *Microcebus*. The two renals are single on both sides, but asymmetrical in the usual way. Into each renal flows on the posterior side an anterior parietal vessel, which corresponds, as I believe, to one of the two veins on each side which accompany the ureter in the Marsupials. On the left side there was also a small vein like that in *Microcebus* closely accompanying the postcaval and flowing into it above close to its junction with the left renal. Posteriorly, I think, but am not quite certain, it joins the spermatic of its side. In this case the likeness to *Microcebus* is quite close. The two principal and

* "The Postcava of an Adult Indian Chevrotain," Anat. Anz. xxix. 1906, p. 375.

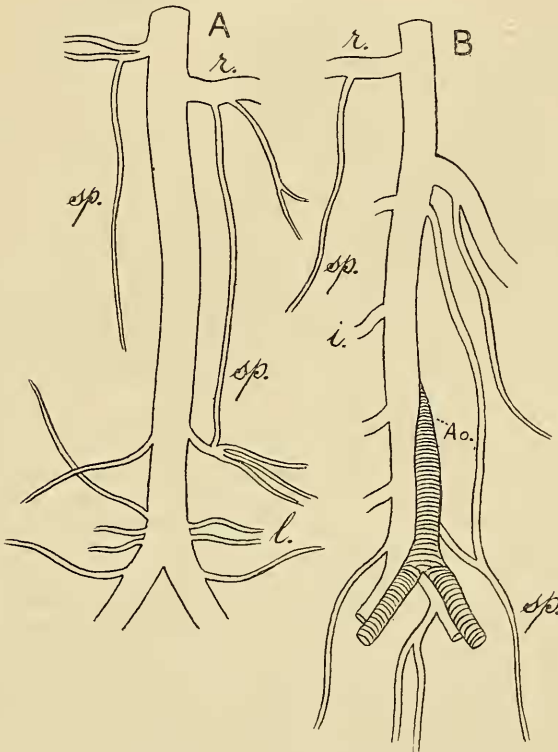
† Amer. Journ. Anat. vol. vii. 1907, p. 111.

‡ P. Z. S. 1908, p. 694.

§ Vide *infra*, p. 521.

posterior spermatic veins flow into the postcava quite far back near to the bifurcation of that vein. They are quite symmetrical. Between the influx of the left renal above and of the spermatic veins below I counted four unpaired intercostal trunks. The iliac veins were asymmetrical, as is shown in the drawing (text-fig. 137), the internal arising as one trunk from the left external iliac.

Text-fig. 137.



Postcaval vein and its branches in *Microcebus smithii* (A) and *Lemur catta* (B).

Ao. Aorta. Other lettering as in text-figs. 132, 133.

In so far as concerns the **Rodentia**, the Rabbit is naturally very well known *; and Hochstetter has furthermore called attention † to several variations in the venous system as affecting the tributaries of the postcaval. On the whole, it would appear that the

* Krause, 'Anatomie des Kaninchens,' Leipsic, 1884; Haswell & Parker, 'Text-book of Zoology,' London; and many similar works.

† Morph. Jahrb. Bd. xx. pp. 585, 586, figs. 7, 8, 9.

several branches of the postcava in that animal are as in the Hystriciform Rodents, of which I give a certain number of details presently. In two out of the three venous systems figured by Hochstetter the left spermatic vein entered the left renal vein, while the right spermatic vein entered the postcaval a good way below the entrance into it of the two renals. A very remarkable state of affairs was shown in a third example which I have not been able to parallel in any Rodent dissected by myself. In this animal the left spermatic artery entered the left parietal lumbar vein.

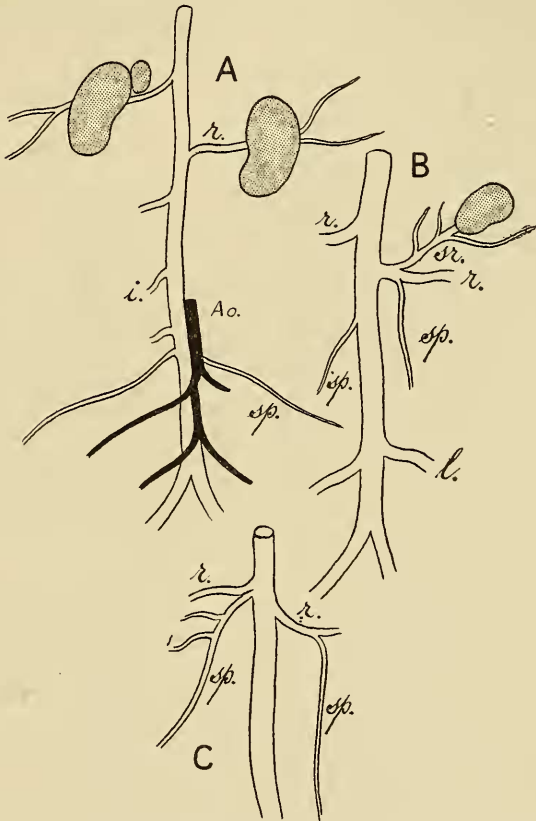
Of *Hystrix cristata* I have examined the postcaval vein and its branches in three examples, in all of which the conditions were much the same but not precisely identical. All the renal veins showed the usual asymmetry, which need not be further particularised. In all, the left ovarian vein entered the left renal vein; in two of the individuals the right ovarian vein entered the postcaval a good way below the entrance of the left renal; in the remaining specimen the point of entrance was higher up on a level with the entrance of the left renal, as in the *Myomorpha* generally. In one specimen (I have no notes upon the other two as concerns this vein) I observed the right lumbar parietal vein to enter the corresponding iliac vein and not the main trunk of the postcaval. In another specimen (again I have no notes upon the matter in the remaining two) the caudal vein was asymmetrical and entered the left iliac.

Chinchilla lanigera is quite like *Hystrix cristata*; in both of two specimens the renals were asymmetrical and the left genital vein entered the left renal, while the right genital vein entered the postcava some way down. An example of *Dasyprocta cristata* showed the same features. A specimen of the Capybara, *Hydrochoerus capybara*, was identical, save for the fact that the renal veins were fairly symmetrical. The left suprarenal vein, it should be mentioned, opened directly into the postcaval vein above the renals. In a second specimen of this Rodent the renal veins were also symmetrical. A specimen of *Aulacodus swindernianus* showed also symmetrical renal veins; the ovarian veins were as in the last three genera. Of the Viscacha, *Lagostomus trichodactylus*, I have dissected the postcava in two specimens. In one the renal veins were about symmetrical; in the other the right was a little in advance of the left. In both specimens the ovarian vein of the left side opened into the corresponding renal, and of the other side into the postcava opposite to the left renal.

The postcaval and its branches in *Hydromys chrysogaster* (text-fig. 138 B) are as follows:—The postcaval itself occupies the usual position to the right of the aorta. The renals are asymmetrical, the left vein opening below the right in position. The left suprarenal vein receives, after leaving the suprarenal body, three parietal veins, two anteriorly and one posteriorly. The left ovarian vein enters the left renal, and the right ovarian vein enters the main trunk of the postcaval not a very great way

behind the entrance of the left renal, the prevailing Eutherian arrangement thus occurring. The lumbar veins are asymmetrical, the left vein debouching into the postcaval above the right.

Text-fig. 138.



Postcaval vein and its branches in *Sciurus prevesti* (A), *Hydromys chrysogaster* (B), and *Dipus hirtipes* (C).

Lettering as in text-figs. 132, 133, 137.

Gerbillus aegyptius and *Zapus hudsonianus* (text-fig. 139, A, B, p. 519), which are both members of the group Myomorpha, but which are placed by Mr. Thomas* in quite different sections of that group, show an interesting point of similarity, of which possibly it is easy to exaggerate the importance as a mark of similarity. Posteriorly in both animals the postcaval vein lies accurately above the aorta

* P. Z. S. 1896, p. 1016.

(i. e. "below" when the animal is dissected, as is usual, from the ventral surface) for some distance in front of the point where it emerges from between the divergent iliac arteries accurately in the middle line. This is, of course, only an exaggeration of the prevailing Eutherian condition. Still it is noteworthy that a new kind of symmetry in the relation of vein and artery precisely the reverse of that characteristic of the Marsupials should be visible in these Murines. Finally, in both of these species the spermatic vein entered the iliac vein of its side, and was thus not directly connected with the postcaval or renal, as is the usual state of affairs in Eutherian Mammals.

In *Georhynchus capensis* (text-fig. 139 C) the veins with which I am concerned in the present communication are different from those of some other Rodents. The renal veins are not situated opposite to each other, the left being below the right. The right ovarian vein is symmetrical with the left renal and passes, like it, almost at right angles to the postcava, the ovary of that side being situated to the outside of and not much behind the kidney. It gives off two branches which run at right angles to it and parallel with the postcava along the ureter and the oviduct. On the left side the ovarian vein joins the left renal, but before it joins receives a vessel running along the oviduct. The renal vein nearer to its embouchure into the postcaval receives a slender vein which runs along the ureter. Posteriorly there is a caudal vein which opens into the left of the two iliac veins which together form the postcaval. *Dipus hirtipes* (text-fig. 138 C, p. 517) does not differ much from *Georhynchus*. But the right ovarian vein flows into the postcaval rather nearer to the right renal.

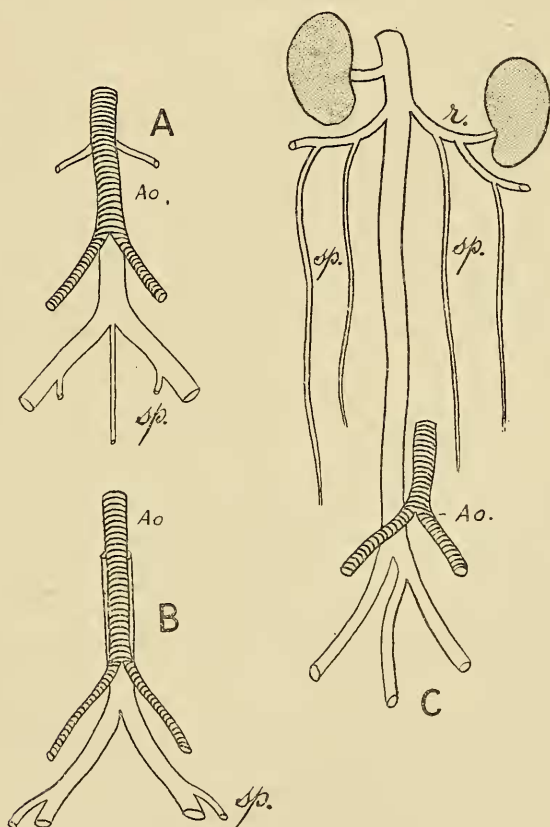
Graphiurus murinus is, in many respects, like *Georhynchus capensis*. The renals are even more asymmetrical, the space of postcava left between their respective mouths being greater. The left suprarenal vein enters the postcava opposite to the right renal. Between the two renals enters the right ovarian vein; this is, as in *Georhynchus*, at right angles or nearly so to the postcaval stem, and, as in the Rodent mentioned, receives an ascending vein which runs along the oviduct. On the left side of the body the ovarian vein enters the left renal; but the latter vein, instead of being at right angles with the postcava or sloping posteriorly, is directed rather anteriorly. This ovarian vein receives an ascending branch as does the right ovarian vein.

In *Sciurus prevosti* (text-fig. 138 A) the renal veins were asymmetrical in the usual fashion. The ovarian veins were symmetrical and situated far back, flowing into the postcaval not far in front of the union of the iliacs. Between these veins and the left renal there were three unpaired intercostal veins. *Sciurus cinereus* was the same, except that the two spermatic veins appeared to open into the postcava by a common stem. In front of this were two lumbar parietal veins, of which the left-hand one was rather the anterior. In *Sciurus maximus* the spermatic veins had the same symmetry and posterior origin.

The posteriorly situated point of opening of the spermatic and ovarian veins in the genus *Sciurus* is, so to speak, a less exaggerated condition of these veins than that found in *Gerbillus* and *Zapus*, and is suggestive of the condition which appears to be universal among the Marsupials.

In *Notiomys cervinus* (of which I have dissected two examples, both females) the renal veins show the usual asymmetry, the

Text-fig. 139.



Postcaval vein and its branches in *Zapus hudsonianus* (A), *Gerbillus aegyptius* (B), and *Georhynchus capensis* (C).

Lettering as in text-figs. 132, 133, 137.

right entering the postcava higher up than the left. In both specimens the right ovarian vein entered the postcaval at a point pretty well opposite to the entrance of the left renal. The left

ovarian vein, on the other hand, entered the left renal. In one of the two examples which I dissected, and of which I took more elaborate notes, a small vessel running along the ureter also entered the left renal. In this specimen the left suprarenal vein before entering the left renal received a branch from the parietes anteriorly, and there were two large lumbar parietal veins entering the postcava before its posterior bifurcation and asymmetrically; the left vein entered the postcava higher up than the right. Although these vessels ran towards the uterus, they did not, as it appeared to me, receive any affluents from any part of the generative system.

In *Mus coucha* the conditions which obtain are very much like those seen in *Notiomys*. The two renals are asymmetrical in the same way and the ovarian veins have precisely the same connections, which, on account of their identity, I need not recapitulate. There are two other veins which correspond in their distribution to the lumbar parietal veins of *Notiomys*, but which are differently connected with the postcaval. On the left side of the body the vein in question enters the left renal to the inside of the point of entrance of the left ovarian vein, but quite independently of it. On the right side of the body this parietal vein has quite a different connection, for it joins the right ovarian vein before the latter debouches into the postcaval vein opposite to the entrance of the left renal.

Otomys irroratus agrees with *Notiomys cervinus* in the disposition of the postcaval and its branches. The two renals are asymmetrical, the left, as usual, being below the right. Into the left renal flows a vein which is composed of two chief affluents, a vein from the ovary itself and a longer vein from the uterus. On the right side the same two veins are present, and form a common trunk which flows into the postcava just opposite to the entrance of the left renal. The two suprarenal veins enter the postcaval independently of the renals. The left suprarenal has a curious course; it actually pierces the liver on its way to join the postcaval. Below the ovarian veins a large lumbar parietal vein on each side joins the postcaval. These are nearly if not quite symmetrical.

In *Arvicanthis pumilus* there are no great differences. The renals are not symmetrical; the left is joined by the ovarian vein, while the right ovarian vein enters the postcaval a little way below the entrance of the left renal.

The few Rodents upon which I am able to report in the present communication very clearly show that this group is by no means so uniform as the American Edentates or Marsupials. It is furthermore plain that the Hystricomorpha present uniform characters in the postcaval vein and its branches. There are no differences of importance among the six genera belonging to this group which I have examined.

The Myomorpha, on the other hand, are by no means so uniform. *Hydromys* is like the Hystricomorpha; *Mus*, *Notiomys*,

Georychus, and some other genera agree closely, while *Zapus* and *Gerbillus* seem to approximate to the Squirrels. Opinions as to the classification of Rodents vary greatly*.

§ *Some Variations of the Postcaval Trunk.*

Under this heading should no doubt strictly be included a very large proportion of the facts with which I deal in the present communication. I limit myself, however, in this section to two cases of apparently abnormal position of the postcava; "abnormal" because they are not like any condition of that vein which is characteristic of a given group or even minor subdivision of any mammalian order. From this point of view, therefore, I cannot include the occasional duplication of the postcaval in *Erinaceus*, since it would appear to be fairly common in that genus, and is also a marked character of the Edentata, &c. Moreover, it might be urged that the single postcaval lying to the right of the aorta is the abnormal condition in *Erinaceus europæus*.

In an example of *Chiromys madagascariensis* dissected in September of last year I found that postrenally the postcaval vein lay to the left instead of to the right of the aorta. The normal condition of this vein has been already and quite recently described by myself †. The arrangement of the spermatic or ovarian veins as the case may be appeared to me to differ in the two sexes, and did undoubtedly differ in the two individuals upon which I reported to the Society. In both individuals the right spermatic or ovarian vein flowed into the postcava rather distally but still some way in front of the posterior bifurcation of that vein. In the female the left ovarian flowed into the left renal, while in the male the corresponding spermatic vein flowed into the postcaval a little way anterior to the entrance of the right spermatic vein. The relative position of these veins in the male is important to be borne in mind. In the abnormal example of *Chiromys* to which I refer in the present communication, the relative position of the two spermatic veins was—in correspondence, as I imagine, with the sinistral postcava—entirely reversed. The right spermatic vein entered the postcava anteriorly to the left.

There was, however, no reversion in the position of the renal veins; they lay exactly as in the two normal examples described by myself. It may be worth while mentioning that in this abnormally veined *Chiromys* the small anterior lumbar parietal vein, to which I directed attention as occupying in the male the position of the ovarian vein in the female, is present; it lies, however, on the opposite side of the renal and therefore ends anteriorly; it is not to be confused with a suprarenal vein. This variation in *Chiromys madagascariensis* seems to be exactly paralleled in a variation of *Homo sapiens* referred to by

* Cf., e. g., Thomas, P. Z. S. 1896, and Tullberg, Nov. Act. Upsala, 1899.

† P. Z. S. 1908, p. 700.

Hochstetter*, where a prevailing left posterior vena cava was accompanied by a right spermatic vein opening into the right renal vein and a left spermatic opening into the postcava itself. This is the exact reverse of the normal conditions obtaining in Man, where, as in so many animals, it is the left genital vein which pours its blood into the left renal while the right-hand vein enters the postcava directly.

I have only examined one example of the American Monkey *Chrysothrix sciureus*, and it is rather remarkable to find that that one specimen, not in any way selected, should show a variation; for so I must in the present state of our knowledge interpret the conditions shown by the postrenal section of the postcaval vein. The vein was in fact, as in *Chiromys* just dealt with, developed on the left side instead of the right. It lay very distinctly to the left of the aorta. Corresponding with this abnormality in the position of the postcaval, its principal branches showed an entirely similar position to those of *Chiromys* and the human abnormality which I have compared with it. For of the two ovarian veins the left entered the main trunk of the postcaval some little way down the latter, while the right ovarian vein poured its contents in the postcaval just below the entrance of the right renal vein. I cannot but think that in the normal arrangement of the veins of this animal the postcaval was on the right side of the aorta and the position of the two ovarian veins was reversed, the left being anterior to the right.

§ *Résumé and General Considerations.*

It is, in the first place, clear from what has been detailed in the foregoing pages, and from my previous papers in which the postcaval system is dealt with, that the postcaval system of veins in Mammals is subject to variations of an individual character. This conclusion is not of course deduced from my own work only, but from what has been written by others which I am able to confirm for other animals and from additional examples of species already known. Even in the very few individuals of certain species which I have been able to dissect, variation has always been noticeable. For instance, in three specimens of *Chiromys* variations occur; in four examples of *Ictonyx capensis*, in three of *Hystrix cristata*, in two specimens of *Erinaceus europæus*, in two of *Suricata tetradactyla*, in three examples of *Dasyurus maculatus*. And these variations together nearly cover the range of variation which the postcaval and its branches show among the Mammalia. In spite, however, of these variations from individual to individual of a given species, there are certain characteristics of groups which may be laid down with some confidence, and with more confidence—I venture to assert—from a consideration of the new facts which I bring forward here.

* *Loc. cit.* p. 638. This paper contains a good many references to the literature of venous abnormalities in man, as well as descriptions of instances.

Thus the Marsupials possess a general character of the post-caval and its branches which is shared by no other group of mammals. Furthermore, it is very noteworthy that within this particular group the variations in important matters is but slight. Thus the only features which differ at all from genus to genus or from species to species are the symmetry or asymmetry of the renals, the exact origin of the suprarenal vein of the left side, whether from the left renal or from an adjacent part of the post-caval, and the freedom or connection by anastomoses of the anterior pair of veins which leave the renals on each side together, and finally their connection or perhaps non-connection by anastomoses with the posterior spermatic veins where they cross them dorsally on their way to the testes or ovaries. It will have been observed that it is quite impossible to distinguish the Carnivorous from the Diprotodont Marsupials by their veins; the whole group of the Marsupials forms an assemblage of which the various members are closely connected in these characters.

So far as facts already known enable us to say, it seems clear that of the Marsupials only an individual of *Trichosurus vulpecula* and the genus *Didelphys*, and in the latter only occasionally and by no means typically, have preserved the earlier condition of the mammalian postcaval system as seen in *Ornithorhynchus* and in *Echidna*, where the postrenal part of that vein is persistently double, being developed out of both collateral veins of the embryo*. This condition is, however, fully characteristic of the Edentata, which form an assemblage apparently quite as distinct in these characters as are the Marsupials. The present communication to the Society allows me to confirm the data of Hochstetter and Hyrtl by fresh examples of species of Dasypodidae. I may also mention that in two examples of *Myrmecophaga jubata* which I have recently dissected the postcaval vein was double postrenally, though I have not made notes of sufficient elaborateness to permit of a detailed account of the facts in the earlier part of this paper. Hochstetter has also stated that *Myrmecophaga* and both of the Sloths †, viz. *Choloepus didactylus* and *Bradypus tridactylus*, possess the same type of postcaval system, and also the Old World Edentate, *Manis* ‡. Judged by the conditions which obtain in the Monotremata, the Edentata are more primitive than are the Marsupials. And, moreover, no Edentate, so far as is known at present, shows the typical Eutherian condition of the veins in question. It is a very singular fact that among the Marsupials the typical Eutherian condition of the postcaval is seen in only one form (*Petaurus tanguanoides*) §, just as the Eutherian placenta is also seen in only one form. We know so little about the Insectivora as regards their venous

* Morph. Jahrb. xx. p. 362, pl. xv., and in Amer. Journ. Anat. ii. pl. iv. figs. 17, 21, &c.

† Morph. Jahrb. xxv. p. 621.

‡ Hyrtl, Denkschr. Ak. Wien, vi. 1854.

§ Morph. Jahrb. xx. pl. xxiii. fig. 26. And, according to McClure, in one example of *Phalanger ursinus*. This of course may be an abnormality.

system that it is rather premature at present to attempt to lay down any statement of general application. But such facts as we have distinctly prove that the Insectivora occupy a somewhat midway position. They are at least commencing to lose the double postrenal caval. Still it is very frequent. Whether Hochstetter's discovery of a similarly divided postcaval in *Pteropus** will prove this condition to be characteristic of the Bats—or at least the Fruit-Bats—remains to be seen, as also whether the Cetacea are largely or mostly thus to be characterised. It can be safely said that the Carnivora† only show remnants of this state of affairs; but such rudiments are not without significance inasmuch as they occur among the Arctoidea, which are perhaps to be regarded as the most primitive among the Carnivora. McClure's interesting discovery, confirmed by myself, of the condition of the postcaval in the Ungulate *Tragulus* adds one Ungulate genus to this same category; but as this group has been but little studied from the present point of view, it would be premature to base any arguments upon the facts. In contradistinction to the groups of mammals already considered, we have the Rodentia, Lemuroidea, and Primates, which invariably show a postcaval vein lying to the right of the aorta postrenally and possessing no fellow upon the opposite side. That variations have been described does not alter the fact that these Eutherian mammals differ from the Eutherian groups already dealt with. It is true that here again the actual facts known require much increase before any generalisations can certainly be made. But the evidence is already sufficient to be seriously considered. It will be noted that those orders of mammals which show a retention of the Monotreme condition are admittedly primitive; and it may be further said generally that the greater or less persistence of this condition is in relation to their position in the series. Thus the Marsupials, Edentates, and Insectivora are, in the opinion of all zoologists, ancient groups. On the other hand, the Ungulates and Carnivora are more advanced in many ways, while the Primates are still more specialized in some respects. It is also noteworthy that of those types among the more modern and specialized groups which show the character under discussion, it is clear that they are more primitive types than are some of their allies. The Chevrotains stand below the Deer and Antelopes, and the Arctoid Carnivores‡ are nearer to the common stem than are the Cats.

The differences observable among the genital veins are not a

* *Ibid.* p. 619 and references there quoted.

† Beddard, P. Z. S. 1909, p. 491, text-fig. 13.

‡ I take this opportunity of stating that in an example of *Mellivora signata* (in fact, the type specimen described by Pocock, *suprà*, p. 394) the postcaval was divided. The division ran up to just behind the entry of the left renal vein, as in an example of *Ictonyx* recently described by myself (*suprà*, p. 491). The right renal vein entered higher up. The ovarian veins were symmetrical and entered the divided postcaval; below them entered the also symmetrical lumbar parietal veins. No ovarian branches entered either renal vein. I have figured these veins in the memoir referred to (*v. suprà*, p. 491, text-fig. 131 A).

little remarkable. The Marsupials seem to be alone among the non-Monotreme Mammals in possessing invariably two pairs of spermatic (or ovarian—for the sex of the individual does not affect these veins) veins, one pair flowing into the postcaval direct and the other pair, often connected on its way with the former, opening into the renal veins. At least, it may safely be said that this is much the prevalent arrangement. And, furthermore, this group is also to be remarked upon as characterised by the symmetry of the posterior spermatic veins, though here the rule is not so universal. In other animals there would appear to be a persistence of either one pair of these veins or of the other; while some instances could almost seem to prove the retention of the left posterior spermatic vein and of the right anterior spermatic vein. The Dasypodidæ are apparently a group in which the posterior spermatic veins are beginning to vanish. Both pairs occur in *Tatusia kappleri* and only the anterior pair in some other forms. The details I have already given and need not recapitulate here. The Insectivora are a group which are in the same condition as the Edentata. In *Centetes*, for example, there is no posterior spermatic vein, while there is such a pair of veins in *Erinaceus europeus* (at least occasionally). The higher Eutherian mammals, so far as they are known, never appear to possess both pairs of spermatic veins. More usually, as I hope to show shortly, the anterior spermatic vein persists on the left side and the posterior on the right. There are, however, a few forms in which it is the posterior pair only which remain, there being apparently in those forms no trace of the anterior pair. Thus in *Tragulius* and *Sciurus* it seems to be obviously the posterior pair which are the only spermatic veins. Furthermore, in those Carnivora (at any rate *Ictonyx* and *Mellivora*) which occasionally present us with a divided postcaval vein, the posterior spermatic veins persist on both sides, are symmetrical, and are the only spermatic veins. But in examples of *Ictonyx* where the postcaval is single and in other Carnivora where no such duplication has been recorded, the conditions are what may be called the typical Eutherian conditions, *i. e.*, the asymmetrical retention of veins.

This asymmetrical retention of veins seems to be connected with the formation of the renal and postrenal sections of the postcaval vein. As seems to be now fairly certain from the investigations of Hochstetter *, Lewis †, McClure ‡, and of Soulié and Bonne §, already referred to, that region of the postcaval in the higher mammals is developed from the right-hand subcardinal (or perhaps collateral cardinal) and right postcardinal only, the left disappearing. The spermatic veins, therefore, on the left side obviously lose their connection with the postcaval through the disappearance of the intermediate veins. When the development is symmetrical, as in *Tragulius*, *Mellivora*, &c., the genital veins

* *Loc. cit.*

† "The Development of the Vena Cava Inferior," Amer. Journ. Anat. i. 1902, p. 229.

‡ *Loc. cit.*

§ *Loc. cit.*

are also necessarily symmetrical. Here are both embryonic veins preserved with their branches, naturally equivalent on both sides of the body. But in the other cases, the spermatic vein of the left side only retains its connection with the cardinal (doubtless through the rich anastomoses which occur in the embryo), and follows the course of that vein anteriorly, opening into the renal in the left side. This point of view is confirmed by a consideration of those cases (of which I have described two in the present communication) where the left subcardinal or cardinal collateral, as the case may be, is converted into the postrenal section of the postcaval; here the conditions of the spermatic veins are precisely reversed, as would be expected on this view. There remain, however, some instances which can perhaps be disposed of on this hypothesis. There is, for example, the single postcaval vein in the genera *Sciurus* and *Zapus*. As to the latter, however, it is quite possible that its median position is significant. It may be that the two veins of the embryo which are connected with the formation of this part of the postcaval have both persisted and fused together, which would at once account for the median position and for the retention of both posterior spermatic veins. In the Squirrel, on the other hand, the postcaval postrenally is distinctly developed to the right of the aorta as in most Mammals. Still we know nothing of the development of the veins in this mammal, and a study of the development might show that there was after all a fusion of right and left veins of the embryo. Besides these cases we have the peculiarly constant mode of connection of the spermatic veins with the postcaval in the Murine Rodents—in many of them at any rate, in *Notiomys* to take a definite example. Here we have a symmetry between the spermatic veins but of a different kind to that which occurs in other animals, save for a few exceptions. The left spermatic opens into the left renal, while the right spermatic is symmetrical with it and therefore does not open into the renal of its side but into the postcaval opposite to the point of entrance of the left renal. In these cases it appears to me that we may have the disappearance of both posterior genital veins and the retention of both anterior veins. This is, of course, in the absence of embryological data sheer surmise; but we already know of cases where this appears more definitely to be the case, such as a number of Armadillos and the Insectivore *Centetes*. I believe that the cases which have now been considered exhaust the variations known to exist in mammals. From an evolutionary point of view it seems likely that the existence of two pairs of spermatic veins is the more primitive state of affairs, since these veins are more numerous in the lower Amniota, and that the prevalent arrangement of these veins as one pair is the later state. This also (it will be observed) agrees with the mutual relations of the groups of mammals which are here dealt with.